

CRANIAL MATERIAL OF OLIGOCENE AND MIOCENE FLAMINGOS : WITH A DESCRIPTION OF A NEW SPECIES FROM AFRICA

By C. J. O. HARRISON & C. A. WALKER

ABSTRACT

Cranial material is available for two mid-Tertiary flamingos, *Phoenicopterus croiseti* from the Oligocene and a new species from the Miocene, and this is compared with skulls of the three Recent genera. The skull of *P. croiseti* from the Upper Oligocene of France is partly reconstructed, using additional material. It is sufficiently distinct from the type species of *Phoenicopterus*, the Recent *P. ruber*, to warrant its designation as the type species of a new genus, *Gervaisia*. Its bill is slender and less decurved than in *Phoenicopterus*, the mandibular symphysis is shorter and the upper jaw is broad to the tip. New flamingo material from the Lower Miocene of Rusinga Island, Kenya, is referred to *Phoenicopterus* on the basis of palate structure. It is specifically distinct from *P. ruber*, the bill-shape being different and the size much smaller, and it is therefore described as a new species, *P. aethiopicus*.

INTRODUCTION

THE RECENT flamingos comprise four species separated into three genera, *Phoenicopterus*, *Phoeniconaias* and *Phoenicoparrus*, the last including both *P. jamesi* and *P. andinus*. *Phoenicopterus ruber* has three separate populations, *P. r. antiquorum* in Eurasia and Africa, *P. r. ruber* in the Caribbean and Central America and *P. r. chilensis* in southern South America. These are sometimes treated as separate species, but their bones differ only in size. All three forms have been used here for comparison but the skull of the last, *Phoenicopterus ruber chilensis*, has been chosen for the figures.

Skulls representing the three genera were available for examination and are shown in lateral view (Fig. 5B-D). These are *Phoenicopterus ruber*, *Phoeniconaias minor* and *Phoenicoparrus jamesi* respectively. The three, in that order, show a progressive modification of the bill, probably linked with different feeding methods. In the first two we know of such differences, *Phoenicopterus ruber* being a more generalized feeder, on minute crustacea for the most part, and *Phoeniconaias minor* a more specialized feeder on blue-green algae. The bill-structure of *Phoenicoparrus* suggests a feeding method involving fine filtering similar to that of *Phoeniconaias*.

The most generalized form, *Phoenicopterus*, has a longer and less angled bill. In the other two the lower mandible is stouter and shorter and is deflected downwards more vertically; the bony structure is more laterally inflated and the mandibular symphysis longer. At the same time the upper jaw is laterally narrow (Fig. 6), and more sharply angled (Fig. 5), while the palatal ridge is a narrower and deeper wedge (Fig. 7). It is apparent that for the three Recent genera the palate and bill structure are diagnostic features, and cranial material of fossil species can be compared with

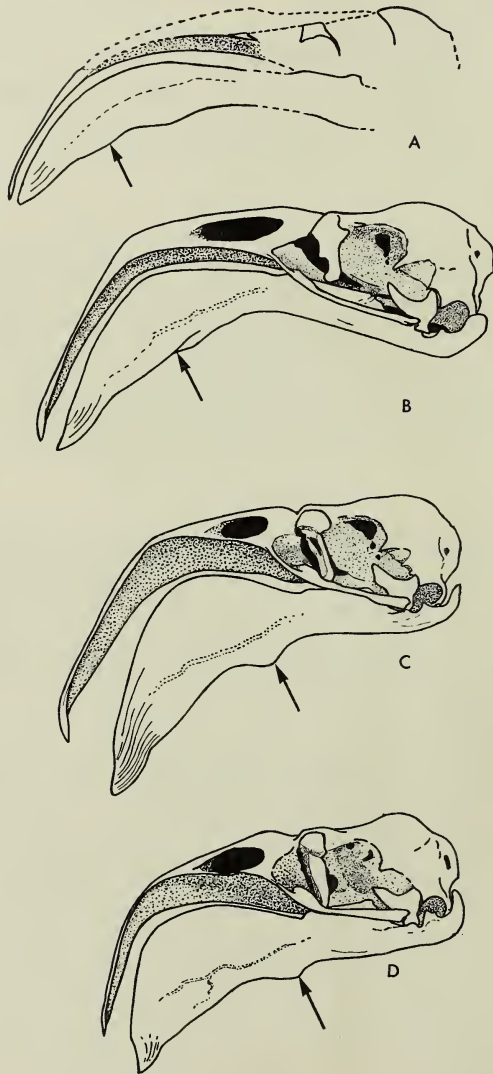


FIG. 5. Lateral views of skulls of: A, *Gervaisia croiseti* (after Gervais); B, *Phoenicopterus ruber chilensis*; C, *Phoeniconaias minor*; D, *Phoenicoparrus jamesi*. The small arrows indicate the posterior margin of the mandibular symphysis; the shaded portions of the upper mandible indicate the area of the palate visible laterally.

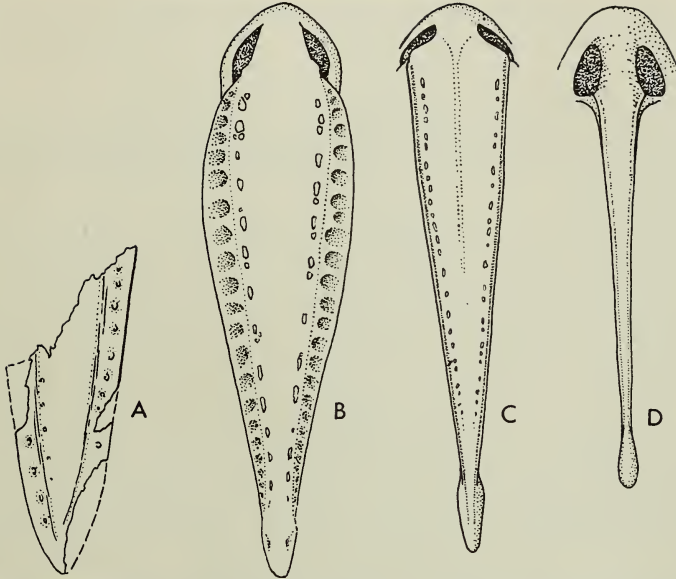


FIG. 6. Anterior views of upper mandibles of: A, *Gervaisia croiseti* (after Gervais); B, *Phoenicopterus ruber chilensis*; C, *Phoeniconaias minor*; D, *Phoenicoparrus jamesi*.

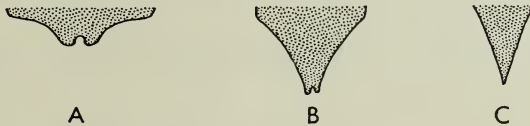


FIG. 7. Transverse section of palate, level with anterior end of nares, of: A, *Phoenicopterus ruber*; B, *Phoeniconaias minor*; C, *Phoenicoparrus jamesi*.

these. Cranial material of fossil flamingos is available for only two forms, *Phoenicopterus croiseti* and a new form from Africa.

GERVAISIA

Phoenicopterus croiseti Gervais 1852

Figs 5A, 6A

P. croiseti was described by Gervais from parts of two skulls and a tarsometatarsus from Clermont-Ferrand and Gergovie, Puy-de-Dôme, France. The deposits at these localities are now thought by Thenius (1959) to be Upper Oligocene and not Lower Miocene as originally stated. More recently a specimen in the collection of the British Museum (Natural History) has been prepared; it is no. A 2665 (*ex*

27827), from the Croiset Collection purchased in 1848, and though said to be collected at Pérignat, France, it is inscribed 'Gergovie'. The preparation has exposed most of the anterior part of a lower mandible and a separate small portion of the posterior end of the mandible in the region of the coronoid process. The mandibular symphysis has undergone some lateral crushing. In shape, size and age the specimen is referable to the present species. With the help of it, using Gervais's plates but not his original specimens, it has been possible to reconstruct part of the skull of *P. croiseti* (Fig. 5A).

The cranial region is too incomplete to be useful, but the bill shows distinctive characters (Figs 5A, 6A). It is longer, narrower and less abruptly decurved than the bills of Recent species. The BM(NH) specimen appears deeper towards the tip of the lower mandible, but the broad tip of the upper jaw, present in Gervais's specimen, may cause the rami of the lower mandible to diverge more sharply dorsally and appear shallower in lateral view. As shown by the BM(NH) specimen the lower mandible is not only narrower and straighter than those of Recent species, with a shorter symphysis as indicated by the small arrows in Fig. 5, but the bony structure is also less inflated. That of *Phoenicopterus* shows distinct lateral inflation of the bone, especially in the deep mid-section of the mandible, and this inflation increases in *Phoenicoparrus* and *Phoeniconaias*. The posterior fragment of lower mandible (A 2665), which includes the coronoid process, has been crushed and provides little information other than that the process appears to have been well developed and that the foramen a little below the process was present.

The palatal ridge of *P. croiseti* is shallow and the upper jaw is down-curved but not angled. The end of the upper jaw differs from those of other flamingos in being broad right to the tip, those of the series of three Recent species listed above showing increased lateral constriction (Fig. 6).

From the shape of the bill *P. croiseti* would appear to have had a more generalized method of feeding than living flamingos. It differs more from the three extant genera than they differ between themselves. If the others are separated into different genera then *croiseti* requires a genus of its own. Apart from the cranial material we have little information on it; the limb bones referred to this species by Gervais (1852), Milne-Edwards (1867-71) and Lydekker (1891) are similar in size and structure to those of *Phoenicopterus ruber* and are not outstandingly diagnostic. The following new genus is proposed.

GERVAISIA gen. nov.

ETYMOLOGY. The genus is named after Paul Gervais who first described the species. It is feminine in gender.

TYPE SPECIES. *Phoenicopterus croiseti* Gervais 1852 : 233-234 ; pl. 2, figs 4-5.

DIAGNOSIS. Bill long and slightly decurved but not angled. Palatal ridge shallow and apparently absent from anterior third of upper jaw. Upper jaw broad and dorsoventrally flattened towards the tip, tapering only gradually. Similar in size to *Phoenicopterus ruber*.

OCCURRENCE. Transitional Oligocene/Miocene deposits of France and Germany (Brodkorb 1963 : 272).

A NEW LOWER MIOCENE AFRICAN FLAMINGO

The collection of the British Museum (Natural History) contains some fragmentary avian material from the Lower Miocene of Rusinga Island in the Kenyan waters of Lake Victoria. A number of these fragments, mostly ends of long bones, appear referable to a single species of small flamingo, similar in size to the Recent *Phoeniconaias minor*. They consist of two mandibular fragments, one proximal and three distal ends of humeri, one distal end of a femur, three distal ends of tibiotarsi, and five proximal and two distal ends of tarsometatarsi. The limb bones, which are mostly broken or crushed to some degree, show little difference from those of *Phoeniconaias minor* save that an almost complete proximal end of a tarsometatarsus shows the calcaneal ridges of the hypotarsus to be similar in proximal view to those of Recent species but only half to two-thirds their length.

The jaw fragments, however, differ more from *Phoeniconaias minor* in their structure. The larger fragment (Figs 8A, 9A) is the posterior part of the upper jaw with most of the narial apertures, embedded in matrix at its posterior end. Its most significant feature is the poorly-developed palatal projection with the double ridge along its centre. In this respect it resembles *Phoenicopterus ruber* so closely that it seems reasonable to include it in that genus (Fig. 9A-B).

The other fragment is from the anterior end of the lower jaw. It is slender, slightly decurved, and heavily grooved in a manner more similar to that of *Phoeniconaias*. It tapers more gradually than does the bill of *Phoenicopterus ruber* in this region and may therefore have been longer and more slender; it appears less deeply hollowed ventrally towards the posterior and in comparison with *P. ruber* the bill may have been shallower in the region of the symphysis. The most marked

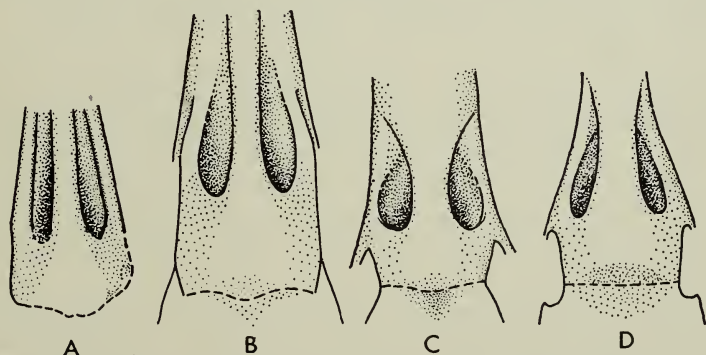


FIG. 8. Dorsal views of basal area of upper mandibles of: A, *Phoenicopterus aethiopicus* (holotype); B, *Phoenicopterus ruber chilensis*; C, *Phoeniconaias minor*; D, *Phoenicoparrus jamesi*.



FIG. 9. Lateral (right) view of posterior part of upper jaw and transverse section of palatal ridges of: A, *Phoenicopterus aethiopicus*; B, *P. ruber chilensis*.



FIG. 10. Transverse section of lower mandible, near tip, of: A, *Phoenicopterus ruber chilensis*; B, *Phoenicopterus aethiopicus* (holotype) partly concealed by matrix.

difference however is in the shape of the tomial edge of this region of the mandible. Recent species of flamingo, and as far as can be determined this applies also to *Gervaisia croiseti*, have a flattened dorsal edge to the tomium on which the flat edge of the upper jaw rests, although the latter is much reduced in *Phoenicoparrus* and *Phoeniconaias*. *Phoenicopterus ruber* has slender, incurving tomia on the lower jaw (Fig. 10A). The new species has stout tomia slanting inwards on the inner surface, with a sharp dorsal ridge, and the outer surface bordering this ridge is laterally compressed to produce a shallow hollow (Fig. 10B). The general appearance suggests that the anterior end of the upper jaw, at present unknown, may have overlapped the lower jaw. If this were so it would constitute a unique feature within the Phoenicopteridae and further taxonomic separation of this species might be justified. For the present, in view of the palatal similarity and the lack of confirmation of possible differences, we propose to treat this as a new species of the genus *Phoenicopterus*.

Phoenicopter aethiopicus sp. nov.

Figs 8A, 9A, 10B; Pl. 6

ETYMOLOGY. The species is named after the continent in which it occurs.

DIAGNOSIS. Small, slightly smaller than *Phoeniconaias minor*. Palatal ridge shallow and double, very similar to that of *Phoenicopter ruber*. Tip of lower jaw narrow, slender and heavily grooved and with stout tomia compressed along the external side to produce a shallow groove, the appearance of which suggests that it might accommodate tomia of upper jaw. Tarsometatarsus with calcaneal ridge of hypotarsus short.

MATERIAL. Holotype: the posterior part of an upper jaw, BM(NH) Pal. Dept. No. A 4382. Paratypes: BM(NH) Nos A 4383-4398, comprising the distal part of a lower jaw, two distal and five proximal ends of tarsometatarsi, three distal ends of tibiotarsi, one distal end of a femur, and three distal and one proximal end of humeri. Most material partly damaged or crushed. Collected and presented by the late Dr L. S. B. Leakey in 1935.

OCCURRENCE. Lower Miocene; locality Rs 12, Rusinga Island, NE Lake Victoria, Kenya.

DESCRIPTION. The holotype is the posterior portion of an upper jaw broken short proximal to the anterior end of the nares, and with some shattering of the internasal bridge. The posterior end terminates at the frontonasal hinge, where it is embedded in matrix. The bone is slender, widening dorsally at the posterior end. The culmen shows only slight curvature and is a little flattened where it terminates posteriorly. The nares are elongated and of fairly even width, rising slightly at the posterior end. The palate is flat posteriorly, with shallow paired ridges present along most of the length and increasing in depth anteriorly.

The anterior end of the lower jaw (A 4384) is within the region of the symphysis and lacks the tip. It is slender, rounded and slightly decurved. Proximally it is flattened and slightly hollowed ventrally. Both ventral surface and sides have many deep longitudinal grooves. The internal surfaces are concealed by matrix, but the interior is deeply hollowed, with incurving tomia. The latter are thicker than those of *P. ruber* and project dorsally, the edges forming dorsal ridges. The sides of the jaw bordering the tomia are laterally compressed to form on each side a shallow hollow with a prominent lower margin, its appearance suggesting that the tomia of the upper jaw may have overlapped it.

On the tarsometatarsus the hypotarsus is very short proximodistally, differing in this respect from those of Recent species and from the similar-sized *P. minutus* Howard 1955 of the Upper Pleistocene of California. The distal end of the tarsometatarsus is like that of *Phoeniconaias*, differing from that of *P. novaehollandiae* A. H. Miller 1963 of the Australian Miocene in the greater spread of trochleae and less clearly indicated articulation for digit 1, from *P. floridanus* Brodkorb 1953 of the Florida Lower Pliocene in the proximally shorter trochlea for digit 2, and *Phoeniconaias gracilis* A. H. Miller 1963 of the Australian Early Pleistocene in the rounder and broader trochlea for digit 2 and more extensive articular surface on the

trochlea for digit 4. The present species also differs from *P. floridanus* in having the distal end of the tibiotarsus narrower posteriorly, and from *P. stocki* L. Miller 1944 of the Mexican Middle Pliocene in being proportionally narrower across the anterior intercondylar groove of this bone. The other known fossil flamingos, *Phoeniconotius eyrensis* A. H. Miller 1963 of the Australian Miocene and *Phoenicopterus copei* Shufeldt 1891 (see Shufeldt 1892) of the American Middle Pleistocene, are both considerably larger species. Except in the matter of size, however, the known differences between these various species are slight, and where critical cranial material is absent it is impossible to assess the true affinities adequately.

MEASUREMENTS. Holotype, A 4382: dorsal length 27.2 mm; ventral length 28.1 mm; depth at posterior end 17.0 mm, at posterior end of nares to tomium 11.5 mm, to palate 14.3 mm, depth at anterior end to tomium 8.5 mm, to palate 11.4 mm; width of nares 5.7 mm; width of posterior nasal strut 5.3 mm.

Anterior portion of lower jaw, A 4384: length 26.1 mm; posterior width 12.4 mm, depth 9.8 mm; width between tomia posteriorly 5.0 mm; anterior width 7.8 mm, depth 7.5 mm; width between tomia anteriorly 4.2 mm; depth of lateral compression bordering tomia 2.2 mm.

Proximal end of tarsometatarsus, A 4383: width at proximal end 14.0 mm; width of hypotarsus 7.9 mm; anteroposterior depth of proximal end to hypotarsus 15.8 mm; depth of cotyla 8.6 mm; proximodistal length of external calcaneal ridge 8.8 mm, of internal ridge 8.6 mm.

ACKNOWLEDGEMENTS

We wish to thank Miss M. L. Holloway of the British Museum (Natural History) for preparing the line drawings.

REFERENCES

- BRODKORB, P. 1953. A Pliocene flamingo from Florida. *Chicago Acad. Sci. nat. Hist. Misc.* 124: 1-4, 2 figs.
- 1963. Catalogue of fossil birds, part 1. *Bull. Fla St. Mus. biol. Sci.*, Gainesville, 74: 179-293.
- GERVAIS, P. 1848-52. *Zoologie et Paléontologie Françaises*, 1. 271 pp. Paris.
- HOWARD, H. 1955. Fossil birds from Manix Lake, California. *Prof. Pap. U.S. geol. Surv.*, Washington, 264-J: 199-206, pl. 50.
- LYDEKKER, R. 1891. *Catalogue of the fossil birds in the British Museum (Nat. Hist.)*. xxvii + 368 pp., 75 figs. London.
- MILLER, A. H. 1963. The fossil flamingos of Australia. *Condor*, Santa Clara, Calif., 65: 289-299, 6 figs.
- MILLER, L. 1944. A Pliocene flamingo from Mexico. *Wilson Bull.*, Sioux City, Iowa, 56: 77-82, 2 figs.
- MILNE-EDWARDS, A. 1867-71. *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*. 474 + 632 pp., atlas 200 pls (2 vols). Paris.
- SHUFELDT, R. W. 1892. A study of the fossil avifauna of the Equus Beds of the Oregon desert. *J. Acad. nat. Sci. Philad.* (2) 9: 389-425, pls 15-17.
- THENIUS, E. 1959. *Handbuch der stratigraphischen Geologie*, 3, Tertiär. Teil 2, Wirbeltierfaunen. xi + 328 pp. Stuttgart.

Dr C. J. O. HARRISON, Ph.D.
Subdepartment of Ornithology
BRITISH MUSEUM (NATURAL HISTORY)
TRING
HERTS

C. A. WALKER
Department of Palaeontology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

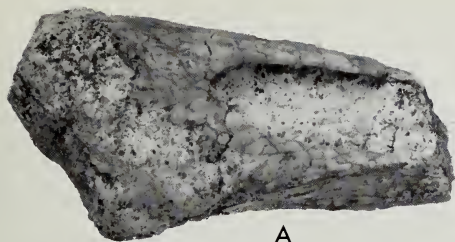
Accepted for publication 9 February 1976

PLATE 6

Phoenicopterus aethiopicus sp. nov.

Holotype, BM(NH) A 4382. Views of the posterior portion of the upper jaw, $\times 2$. A, right lateral. B, left lateral. C, dorsal. D, palatal.

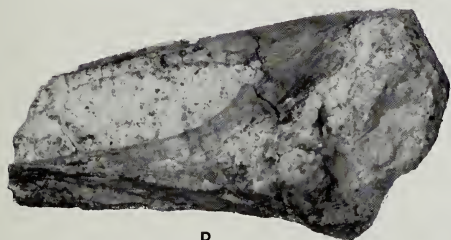
Paratype, BM(NH) A 4383. Views of the proximal end of a right tarsometatarsus, $\times 2$. E, external. F, internal. G, proximal.



A



D



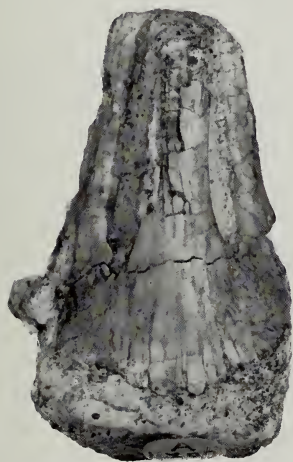
B



E



F



C



G